

ANATOMY OF THE VEGETATIVE ORGANS OF THE SUGAR BEET¹

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INTRODUCTION

The first critical description of the structure of the sugar beet was published by van Tieghem (15).² He traced the ontogeny of the primary tissues and the mode of origin of the supernumerary cambiums and the endodermis, deriving both these tissues from the pericycle.

Later investigators—de Bary (1), Morot (7, p. 241), Fron (5), and Strasburger (14)—mainly substantiated the work of van Tieghem.

As the early investigations were chiefly concerned with the origin and nature of the anomalous growth of the beet, they were naturally limited in their scope. An insight into the organization of the plant in its entirety was given by Droysen (4) and de Vries (16), and the work of the latter has remained a classic to the present day.

As the sugar beet gained in importance as an economic plant, a series of both technical and popular papers appeared dealing with certain features of the beet structure. The popular articles were largely by Briem (2), and were intended to give information to beet growers. Of the purely scientific papers, the account of Wiesner (17) deserves first mention. This contains an accurate description and classification of the different tissues of the beet, with special emphasis on the composition of the walls of the storage parenchyma. An understanding of the localization of the sugar in the different tissues was obtained through the researches of Peklo (8) and Colin and Grandsire (3).

Numerous attempts were made to correlate anatomical structure and sugar content, in the hope of arriving at better methods of selection in breeding for higher sugar content. The futility of these attempts is shown by the contradictory evidence obtained by Schindler (11), Briem (2), Schneider (12), Peklo (8), Geschwind (6), and numerous others.

Certain features of the anatomical structure have been critically reinvestigated in the last two decades. Through the work of Plaut (9), Rüggeberg (10), and Seeliger (13) there is now a correct understanding of the structure and distribution of the endodermis, the fate of the primary cortex, and the development of the primary and secondary tissues of the beet. The detailed and painstaking investigations of Seeliger have led to a modification of van Tieghem's concept of the origin of the supernumerary cambiums which had been taken over unreservedly by other investigators.

The object of the present paper is to give a compendium in the English language of the present knowledge of the structure of the

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² Reference is made by number (*italic*) to "Literature cited," p. 175.

sugar beet. The results of earlier investigations, carried on by different writers and at different times, were in need of testing; and further investigations were necessary in order that there might be obtained a picture of the inner organization of the beet which would be in harmony with present ideas. Comparative studies, so necessary for the proper evaluation of the normal anatomical picture, were limited to imperative requirements, but they will be extended by subsequent investigations.

MATERIAL AND METHODS

The material was obtained partly from seedlings grown in the greenhouse, and partly from beets growing in the field in Colorado. The material was fixed with Flemming's medium solution and stained: (a) Delafield's haematoxylin and safranin, (b) Haidenhain's haematoxylin and safranin, (c) analine blue and safranin. Free-hand sections were examined in chloriodide of zinc or stained with phloroglucin and hydrochloric acid counterstained with chloriodide of zinc. Cork membranes were stained with Sudan glycerin.

All drawings are from photomicrographs, which were taken on Wratten M plates with B 58 and E 22 filters used singly and in combination.

GROSS MORPHOLOGY

Beta vulgaris L. is a herbaceous dicotyledon, a member of the Chenopodiaceae. It normally completes its vegetative cycle in two years. During the first year it develops a large succulent taproot in which much reserve food is stored, and during the second year it produces flowers and fruits.

The mature beet is an elongated pear-shaped body composed morphologically of three regions—the crown, the neck, and the root. The crown is the broadened, somewhat cone-shaped apex. It bears a tuft of large succulent leaves and leaf bases. Adjoining it is the neck, a smooth narrow zone which is the broadest part of the beet and which constitutes ontogenetically the thickened hypocotyl. The root region, which forms by far the bulk of the beet tissues, is cone-shaped and terminates in a slender taproot. It is flattened on two sides, and often is more or less markedly grooved. The two depressions extend vertically downward or form a shallow spiral, and contain the lateral rootlets indistinctly arranged in two double rows. The surface of the beet is covered by a thin cork layer yellowish-white in color except on the aerial parts and at places of injury.

A well-formed beet has only one taproot. Occasionally the taproot branches and forms a number of thick stubby roots. The lateral roots are filiform, and originate from the two-arch xylem plate or from more peripheral rings of growth.

The leaves are arranged on the crown in a close spiral with the divergence of 5/13. The cotyledons, however, are arranged in opposite and decussating pairs. The lamina of the leaf is elongate triangular with rounded tip and undulate margin; the base is cordate and decurrent on the petiole, the latter being triangular in cross section and more or less flattened at the base. The venation is of the netted type. Lateral branches arise from a strongly developed midrib. These run obliquely outward, but before reaching the periphery they bend abruptly, run parallel with the surface, and

unite with the terminal ends of other lateral veins. The smaller veins anastomose freely, with the ultimate branches ending blindly in the parenchyma of the intercostal fields (fig. 1, A, B; fig. 10, B).

Unlike most cultivated plants, the beet shows a striking lack of uniformity in foliage characters. The most diverse types may be found growing side by side; plants with erect or flat foliage; short or long petioles, with lamina triangular or oblong; and straight or wavy margin and smooth or crinkly surfaces. There is also a great variation in the texture and thickness of the leaves as well as in the color, which may be either a dark green or a light olive, with numerous gradations between the two. When this paper was written investigations were underway with the object of isolating distinct foliage types in the hope of getting them sufficiently pure to breed true to form.

ANATOMY

STRUCTURE OF THE MATURE BEET

A median horizontal section through a mature beet shows a number of annular zones or rings of growth which are more or less equidistant, except near the periphery where they are very close together (fig. 2, A, B). Often, instead of a complete ring, smaller or larger segments of rings appear here and there; these are connected by their margin to the next inner ring. The center of the cross section is occupied by a two-lobed, more or less star-shaped core (fig. 3) from which radiate horizontal strands of vascular tissue—the root traces.

Each annular zone of growth is made up of a narrow ring of vascular tissue and a broad band of storage parenchyma. The ring of vascular tissue is composed of numerous collateral bundles separated from one another by medullary-ray tissue of varying width (fig. 4). In median longitudinal section the bundles of an individual ring are seen to anastomose tangentially, and between the bundles of successive rings there are obliquely descending radial connecting bundles. In the narrow tapering zone of the beet the number of annular rings decreases as the rings gradually unite with one another. A union of the rings is also effected in the apical leaf-bearing end, but here it is brought about by the passing out of the leaf traces. Each leaf is supplied with a number of traces of different degrees of development. The central trace extends horizontally through the complete radius of the cross section; the lateral traces do not extend so far, or they may even remain at the periphery. Owing to this arrangement, as pointed out by de Vries (16), the traces of one and the same leaf attach themselves to different annular rings, and, since they also tend to anastomose with one another, the relationship between all the leaves and the annular rings becomes very intimate.

The neck of the beet has, on the whole, root structure, except that in the upper region the central core opens up and incloses pith. As the neck passes into the crown this pith widens and frequently becomes hollow.

The composition of the vascular tissue is more or less alike for all bundles, with the exception of the central core and the peripheral region. The latter, however, differs only in that its bundles are immature, often represented only by undifferentiated cambium. The central core, on the other hand, exhibits a fundamental difference in that it contains both primary and secondary tissues. Its composition will be described in detail under development.

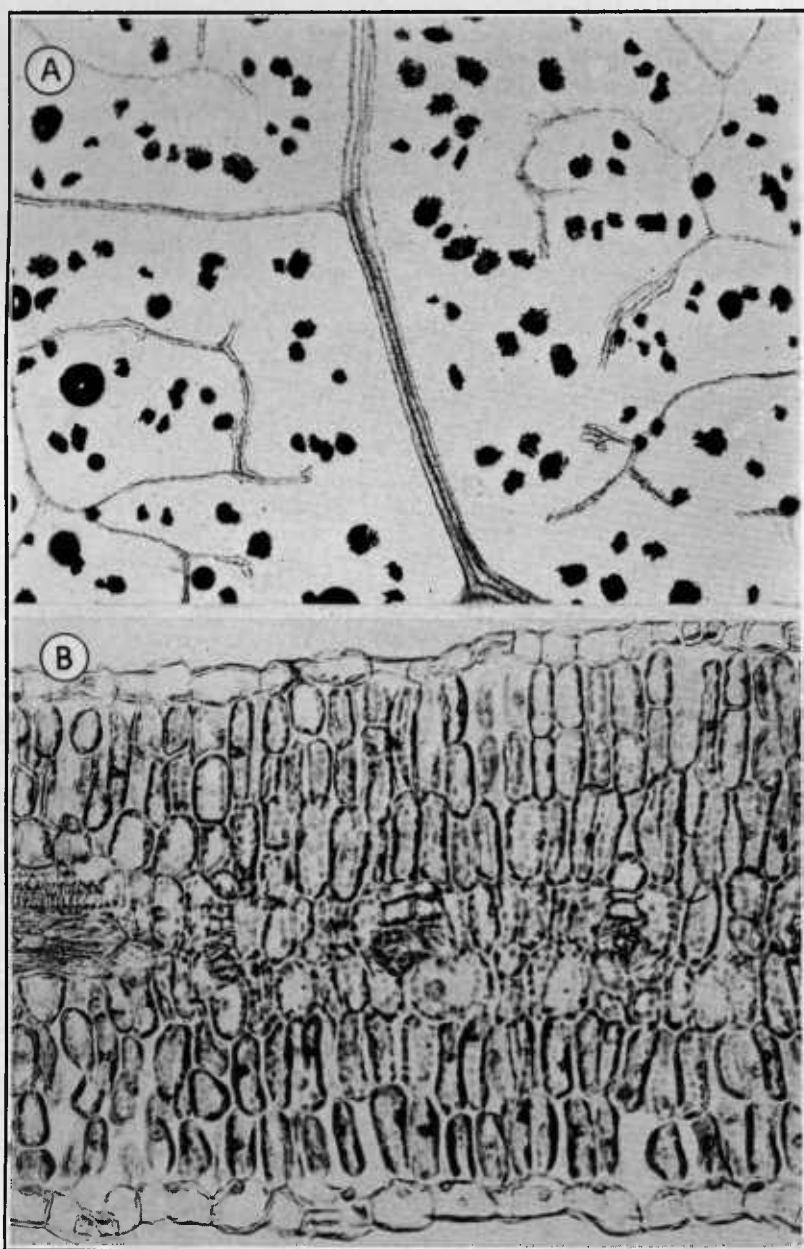


FIG. 1.—*A.* Part of beet leaf bleached to show venation. Note appearance of terminal veins ending blindly in the parenchyma. Dark spots are aggregates of calcium oxalate located in certain cells of the central mesophyll. $\times 66$. *B.* Cross section through a thick leaf. Note that all of the mesophyll consists of palisade cells. $\times 272$

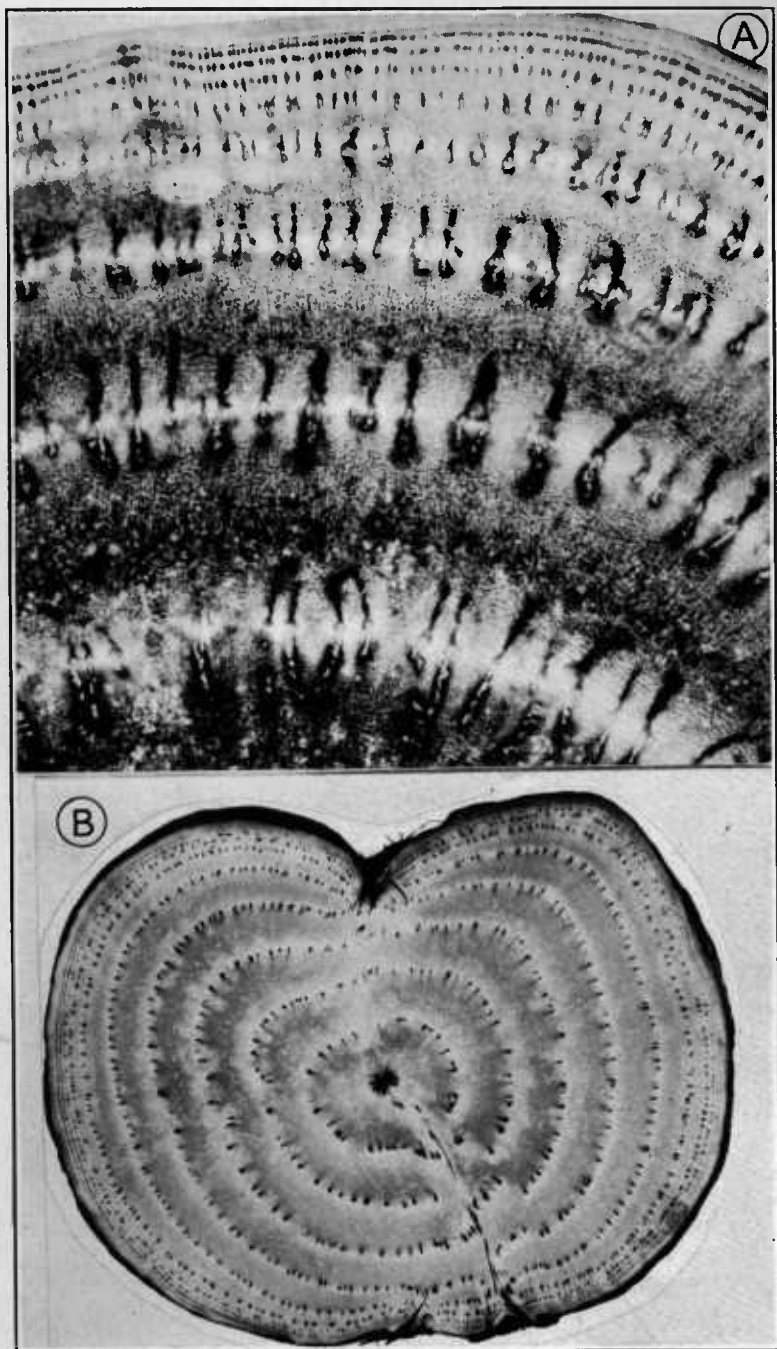


FIG. 12.—A. Partial cross section of a mature beet. $\times 475$. B. Cross section of mature beet, natural size. Section treated with phloroglucin-hydrochloric acid to bring out the vascular bundles

The bundles of the mature rings are widest in the region of the cambium and taper gradually toward the phloem and xylem pole. This gives them the appearance of a double wedge.

The xylem is formed of a radial row of vessels with some lateral thick-walled tracheids and wood parenchyma (fig. 5, A, B). Fibers are found in only the oldest rings of the hypocotyl. The vessels are reticulate; the large ones are porous and have short articulations; the cross walls are strictly transverse but often sloping. The small vessels are more like tracheids, much pointed but porous. Typical tracheids are found only occasionally. The wood parenchyma is elongated and pointed, sometimes cross septate. The walls are perforated by numerous pits; the latter are round, sometimes lathyrate. The fibers, whenever they occur, are elongated and intertwine with their tips. In cross section the fibers are round or prismatic. The cells surrounding the xylem are thick walled and collenchymatous and lack intercellular spaces.

The phloem is composed of sieve tubes, companion cells, and phloem parenchyma (fig. 6, A, B; fig. 7, A). The sieve tubes have terminal as well as lateral sieve plates (fig. 7, B), which soon become covered with callus. The companion cells are of the same length as the sieve tubes, but sometimes they become cross septate. The phloem parenchyma cells are elongated and pointed, often also cross septate. There are numerous cells transitional to the typical storage parenchyma. The walls of the phloem parenchyma cells are strongly pitted, and the corners of all three types of phloem cells are more or less collenchymatously thickened.

The first-formed phloem groups of a bundle are seen as small obliterated areas recognizable only by their staining reaction. They occur commonly at some distance from the bundle due to enlargement and division in the phloem parenchyma.

Between the different bundles of a ring lies a narrow band of intermediate tissue, which, with reference to the bundle itself, is like a normal medullary ray. The parenchyma of these rays consists of radially elongated cells which undergo tangential divisions as the annular zones increase in diameter. Secondary medullary rays frequently develop inside the vascular bundles, causing a forking of the latter.

The concentric rings of vascular tissue are separated from one another by broad bands of storage parenchyma. The cells are large and almost spherical, the walls thin and extensively pitted. The outer and inner peripheries of this interzonal parenchyma contain vascular elements in addition; the outer periphery scattered xylem cells, the inner periphery obliterated phloem.

The lateral roots of the beet are very thin and are covered for a considerable distance with root hairs. The anatomical picture of root structure in these roots differs from that of the thickened taproot in a preponderance of xylem cells, especially vessels (fig. 8). Ray parenchyma is practically wanting. Often the primary xylem plate is triarch instead of diarch, as is always the case in the taproot.

STRUCTURE OF THE LEAF

As seen in cross section, the vascular tissue of the petiole (fig. 9, A, B) forms a triangle which gradually widens basipetally. The number of bundles varies with the size and development of the leaf.

As the petiole merges into the midrib the number of bundles decreases, in that progressively more and more bundles fuse with one another. The large bundles of the petiole run separately from the base of the petiole to the insertion point of the lamina, while the smaller ones anastomose freely and form a network of wide meshes. The bundles are surrounded on all sides by cortical tissue which merges into col-

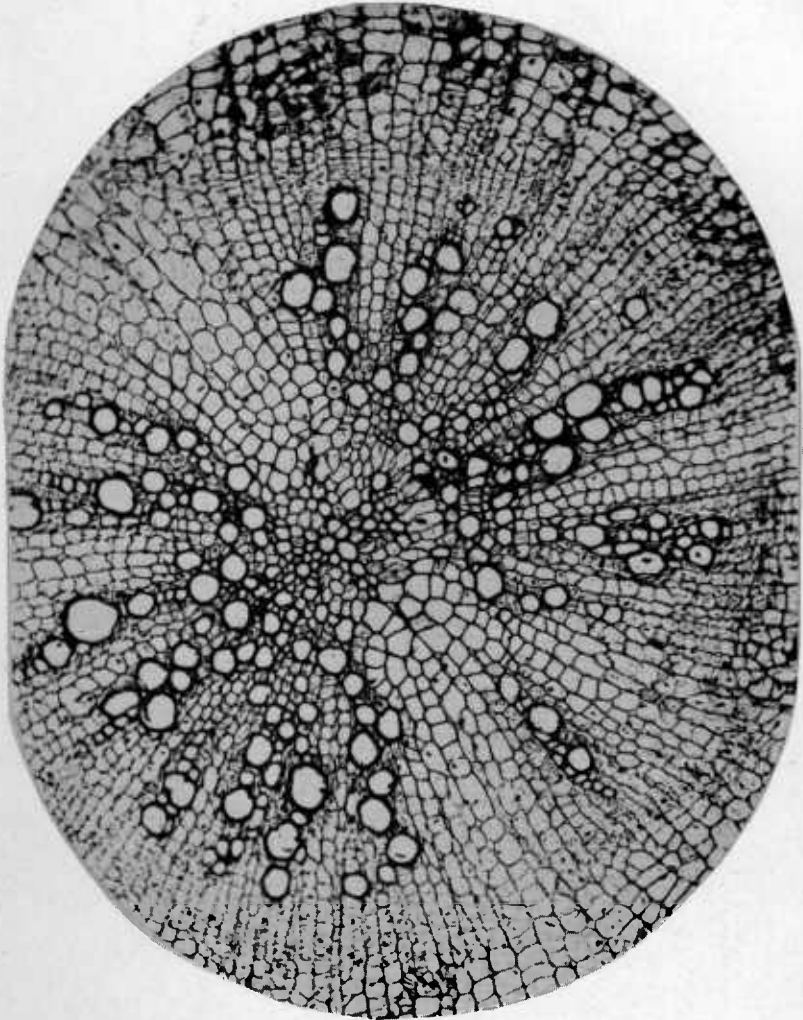


FIG. 3.—Central core of a young, actively growing beet. $\times 118$

lenchyma just beneath the epidermis. The extent and distribution of the collenchyma can best be seen in Figure 9, A. This tissue forms a continuous band near the center of the abaxial surface and is otherwise limited to the projecting ridges. In the midrib it forms a continuous layer on both upper and lower surface.

The epidermis of the petiole is made up of elongated rectangular cells where it covers the collenchyma, and of somewhat elongated,

more or less polygonal, cells where it abuts directly on cortical parenchyma. The epidermis contains numerous stomates (fig. 10, A), except in the regions of collenchyma development. The cells of the

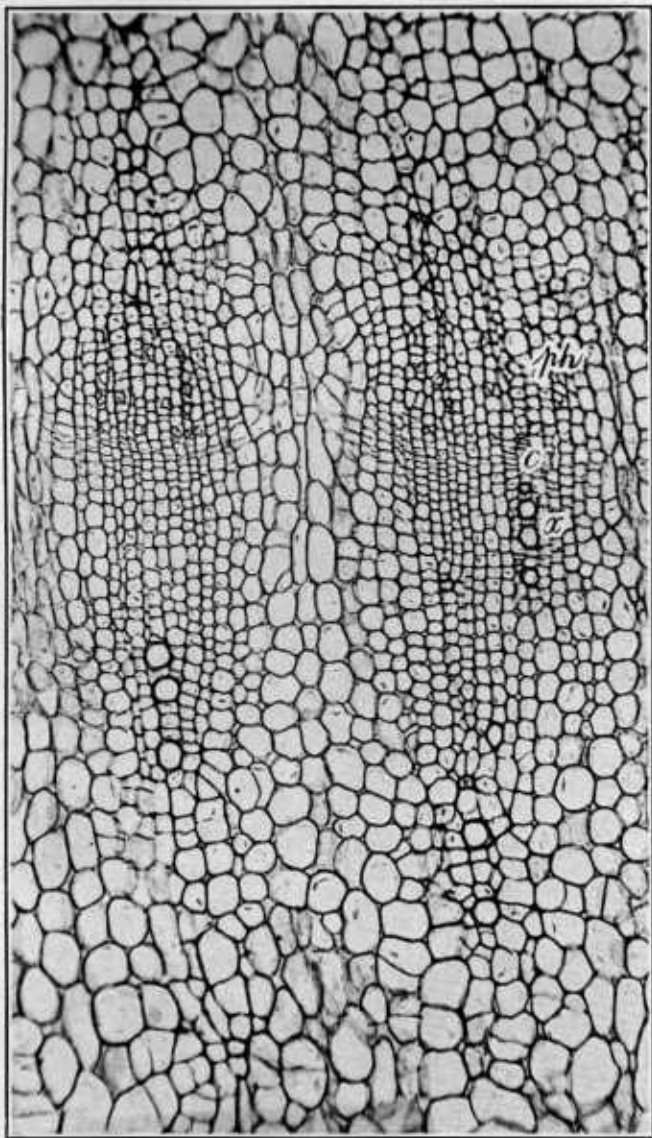


FIG. 4.—Vascular bundles from the outer zone of mature beet. *ph*, phloem; *c*, cambium; *x*, xylem, $\times 100$

petiolar cortex are large, more or less barrel shaped, and are separated by large intercellular spaces. The peripheral cells contain chlorophyll; others, more or less scattered throughout the tissue of the petiole, contain crystal sand.

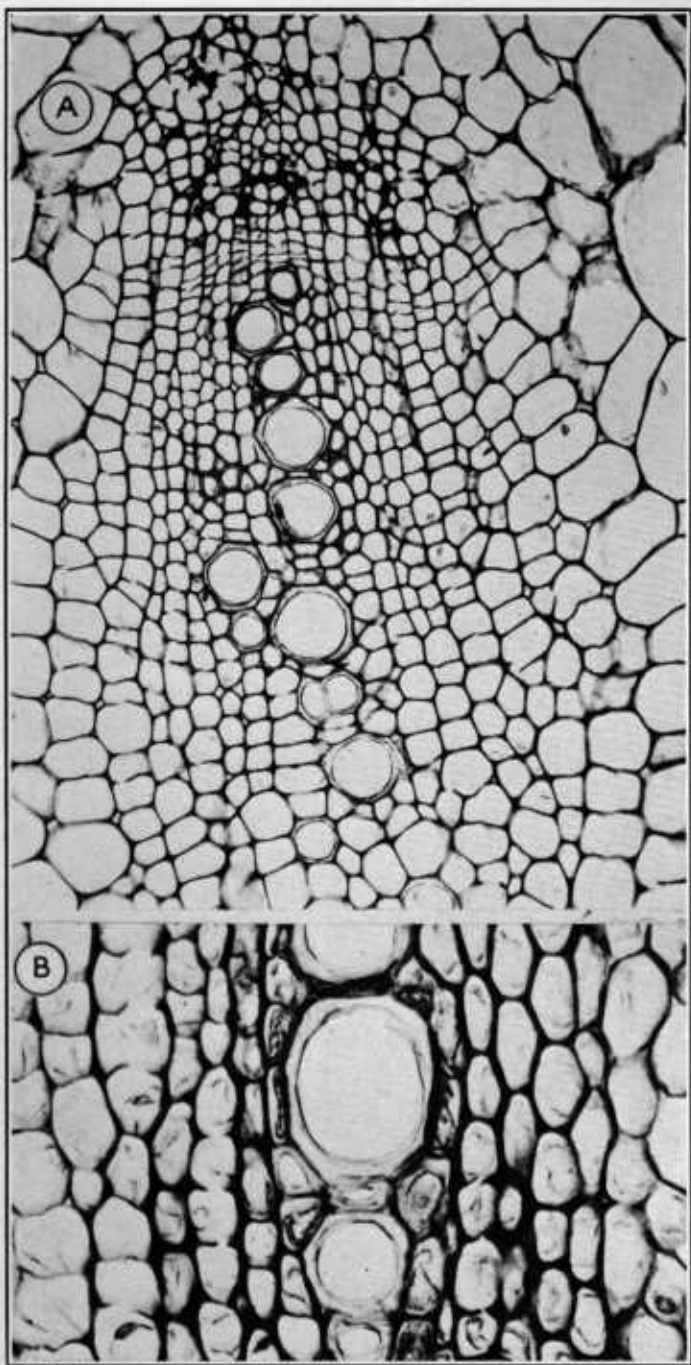


FIG. 5.—A. Typical bundle from mature beet. The sieve tubes show callus deposit and partial degeneration. $\times 170$. B. Partial cross section of mature bundle. The parenchyma cells next to the xylem are thick walled and are spoken of as "sugar-sheath." $\times 500$

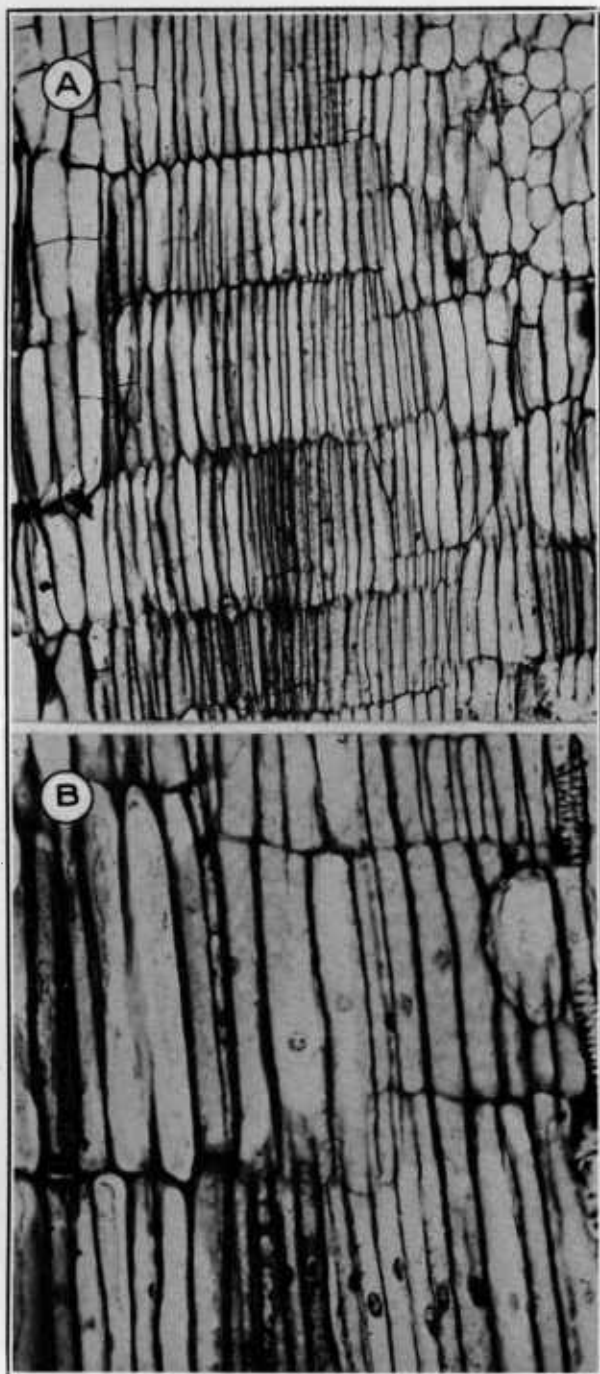


FIG. 6.—A. Radial section of phloem and cambium of actively growing ring. $\times 100$. B. Radial section of phloem and cambium. $\times 260$

The histological composition of the vascular tissue is that of typical collateral bundles. The phloem forms a narrow zone composed chiefly of sieve tubes with their companion cells and some phloem parenchyma. Above the phloem is a large sclerenchyma cap (fig. 11). A much less developed cap consisting of elongated thick-walled cells is found on the xylem pole of the bundle. Adjoining the latter is the protoxylem, interspersed with thin-walled fibers. The secondary wood forms a thick layer composed of numerous wide and narrow vessels and thick-walled fibers. Between xylem and phloem is the cambium formed of regular rectangular cells.

The epidermis of the lamina is unusual in being similar on both surfaces. The upper surface has irregular polygonal cells with tortuous walls (fig. 10, A). Toward the apex the cells become smaller. Here and there are small polygonal cells, the remains of young ephemeral hairs. In certain types of beets the mature leaves have very long, multicellular hairs, especially along the veins. Such leaves were sent to the writer from Rocky Ford, Colo., by A. W. Skuderna, who finds associated with this hairiness a high resistance to the leaf-spot disease. The cells of the lower epidermis are slightly more

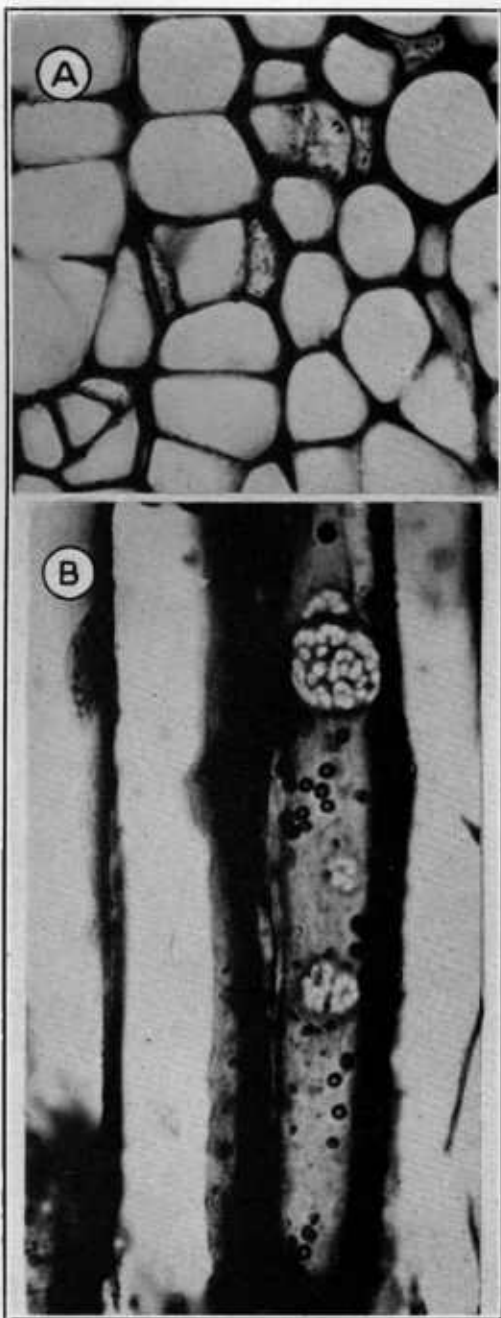


FIG. 7.—A. Mature phloem; the companion cells show granular content. $\times 1,000$. B. Mature sieve tube with lateral sieve plates. $\times 1,000$

irregular and the walls more tortuous. The stomates are of a simple type. The pores are surrounded by a pair of specialized guard cells which contain numerous ehloroplasts. There are no accessory cells.

Stomates are found on both upper and lower surfaces (fig. 10, C), but are more numerous on the lower. De Vries (16) found on the upper surface an average of 91, and on the lower an average of 144

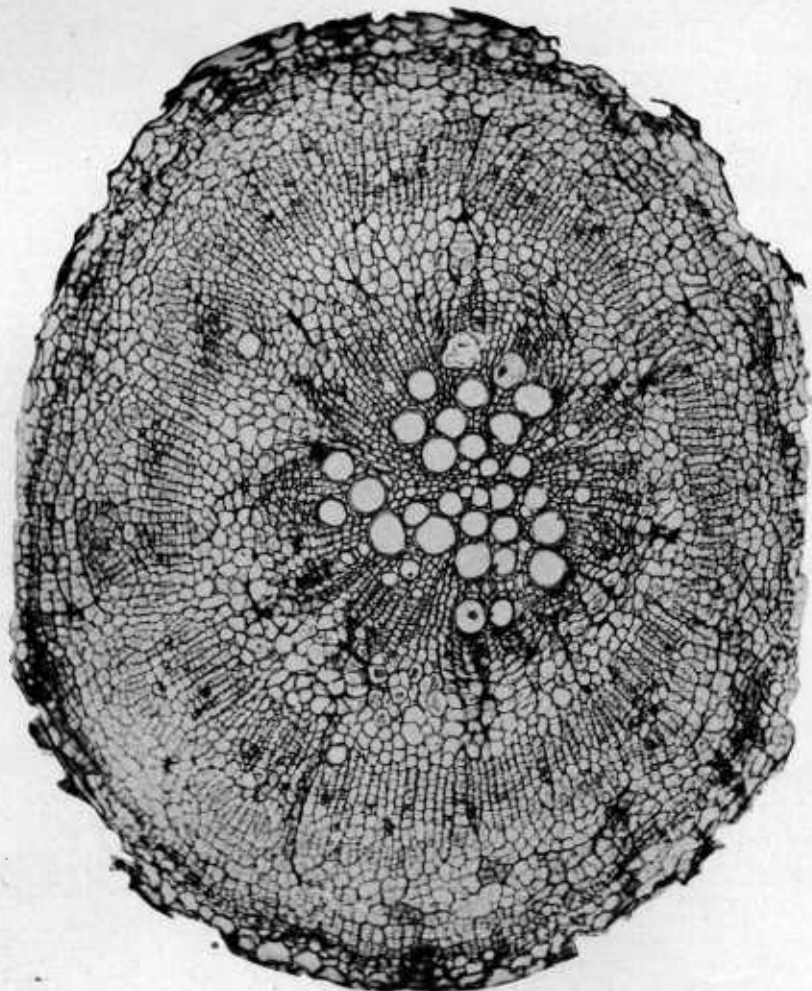


FIG. 8.—Cross section through tip of taproot. $\times 77$

per square millimeter. Droysen (4) found 114 and 162, respectively.

In determining the number of stomates only the degree of maturity of a leaf appears to be a factor. The size of the leaf as well as the different local areas of the lamina—apex, base, margin, middle—play a lesser rôle. It was found that the regional distribution shows as great variation as the fluctuation within the local areas themselves. Young leaves have naturally the largest number of stomates; as many

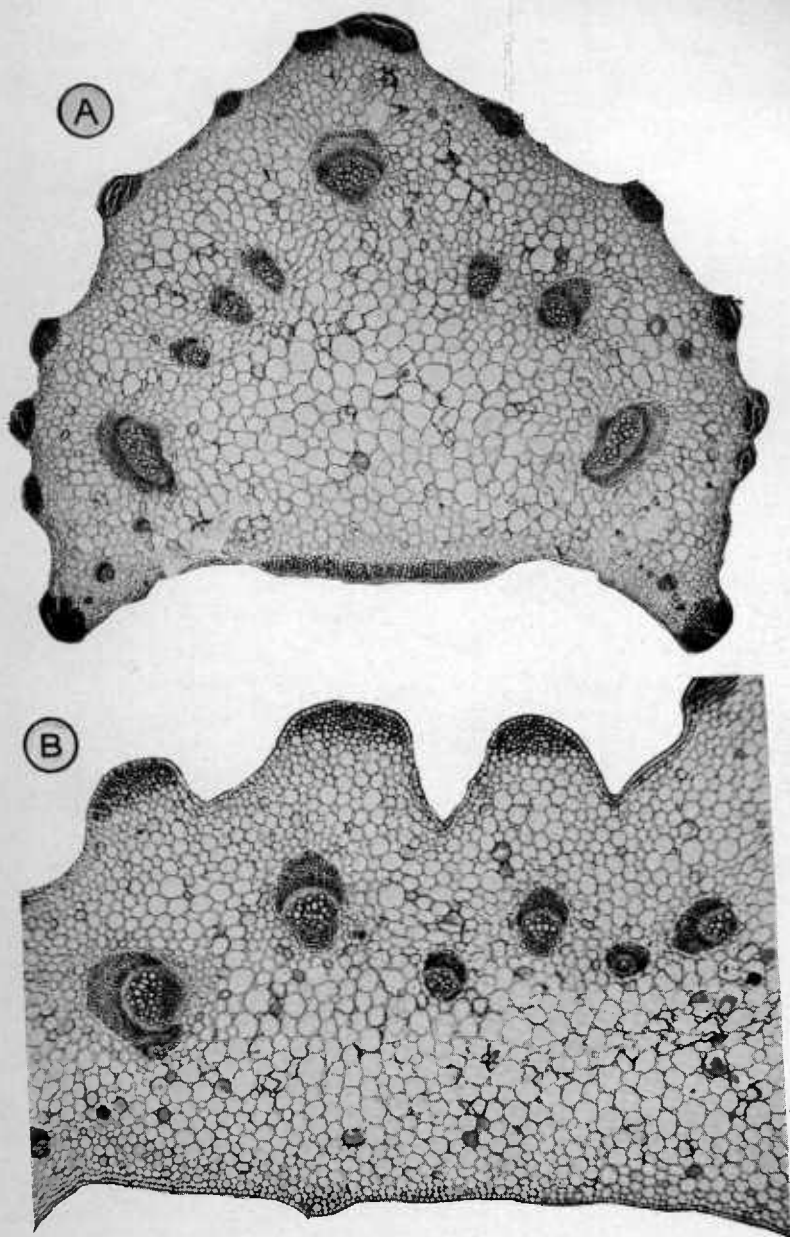


FIG. 9.—A. Cross section of petiole near the lamina. $\times 18$. B. Partial cross section of basal petiole. $\times 28$

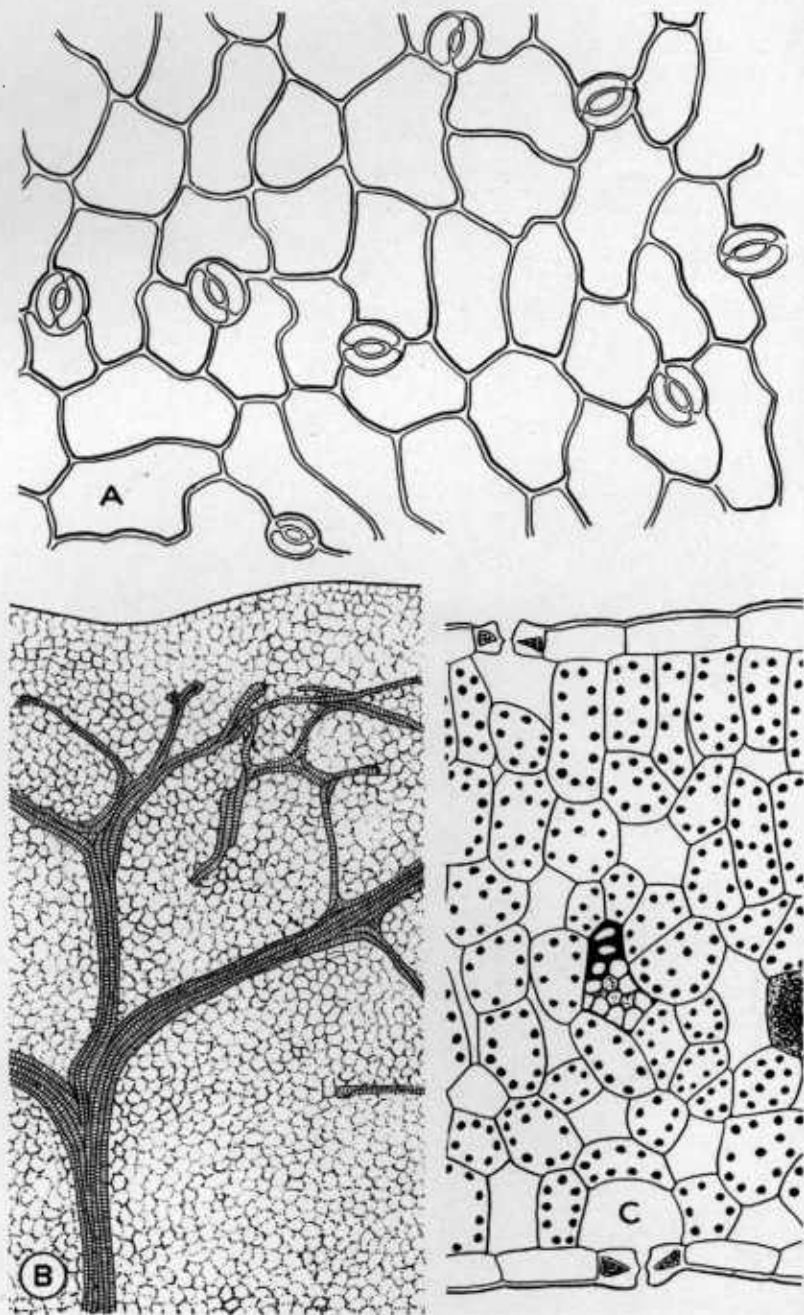


FIG. 10.—A. Upper epidermis, with stomates of mature leaf. $\times 296$. B. Margin of leaf with terminal veins. $\times 90$. C. Cross section of mature leaf [diagrammatic]. $\times 240$

as 300 and more have been counted per square millimeter. These large counts are due to the fact that the epidermal cells are very small and that the stomates have not expanded to their full size. In seemingly fully developed, though still young leaves, the number

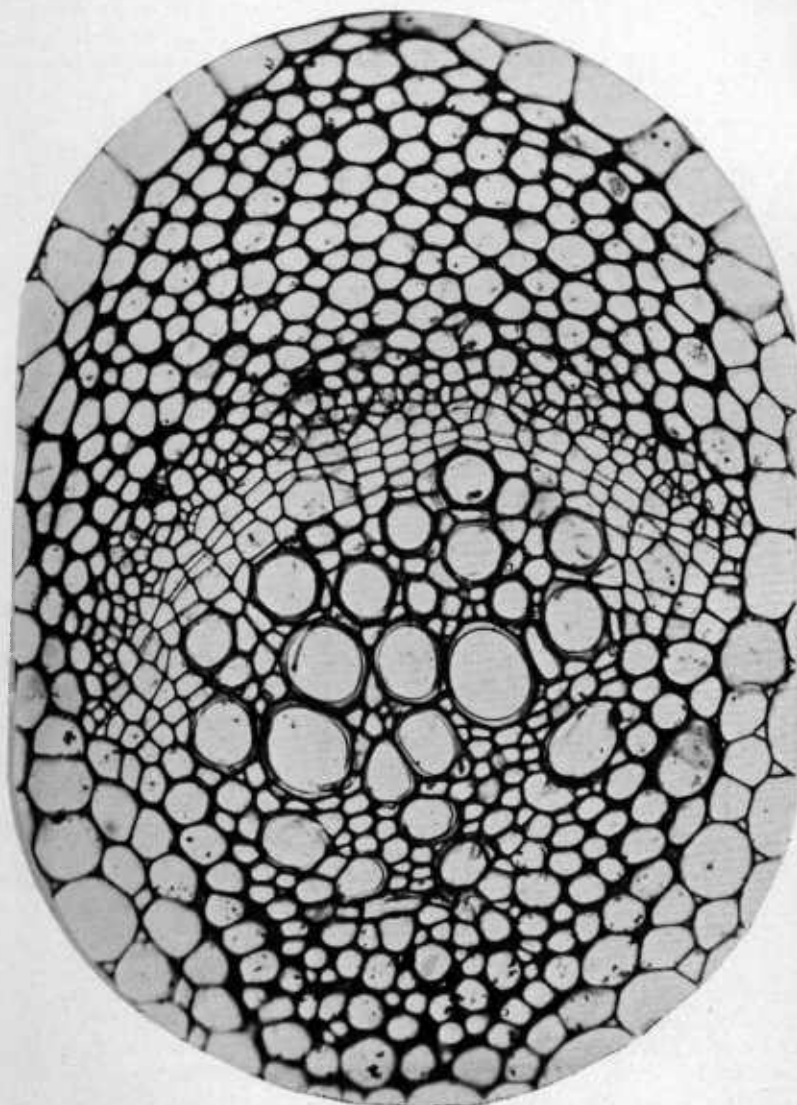


FIG. 11.—Cross section of petiolar bundle. $\times 303$

is still often quite high, with a maximum count of 240 on the lower surface. In fully matured leaves the number is less, but shows a great deal of fluctuation in the different foliage types. Table 1 gives the number of stomates on upper and lower surfaces of leaves of different color, size, and thickness.

TABLE 1.—Color, size, and thickness of leaves, and number of stomates

Color and size of leaf	Thickness of leaf	Number of stomates per square millimeter	
		Upper surface	Lower surface
	<i>Mm.</i>		
Light green; medium.....	0.32	104	122
Light green; large.....	.48	100	111
Medium green; medium.....	.35	130	145
Light green.....	.58	74	97
Dark green; large.....	.48	75	90
Dark green; very large.....	.56	60	59
Dark green; medium.....	.28	73	79
Medium green.....	.41	57	76
Light green.....	.36	90	114
Dark green.....	.45	76	119
Light green.....	.41	77	99
Light green.....	.40	138	167
Dark green.....	.72	88	111
Light green.....	.64	73	113
Dark green.....	.36	103	116
Dark green.....	.45	69	75

According to de Vries (16) and Droysen (4), the size of the stomates on the upper surface is 23 by 32 microns, while the size of those on the lower surface is a trifle smaller. Although these figures represent an acceptable mean, there is nevertheless quite a fluctuation in size in the different parts of a leaf and in different foliage types. Very old leaves have very large stomates, sometimes as long as 45 microns.

The mesophyll of the leaf is formed of parenchymatous tissue, the cells of which contain chloroplasts (fig. 10, C) and occasionally crystal sand. It is normally indistinctly divided into palisade tissue and spongy parenchyma. The palisade tissue is made up of small, more or less cylindrical cells; the cells of the spongy parenchyma are slightly larger and roundish in form.

The number of cell layers in a cross section of a leaf is practically constant, even though the thickness of the leaf varies greatly. In very thick leaves all cells are elongated into a uniform palisade tissue (fig. 1, B), whereas in very thin leaves typical palisade cells are altogether absent and the entire mesophyll consists of very short, roundish cells.

ONTOGENY

Microscopically, the young seedling shows three regions: Root, hypocotyl, and cotyledons. The junction between hypocotyl and root is indicated by an abrupt tapering of the axis and the appearance of lateral rootlets. In very young seedlings this demarcation is less distinct. Seeliger (13) includes in the root the region from the root-cap to the piliferous zone, while the hypocotyl extends from the piliferous zone to the insertion point of the cotyledons.

The cotyledons are elongate elliptical, with the lamina narrowing at the base to form a short petiole. The anatomical structure is very simple. The tissue of the lamina is indistinctly divided into chlorophyll-bearing palisade cells and spongy parenchyma. The

latter contains numerous calcium oxalate cells. The epidermis is simple, and is composed of irregular polygonal cells with somewhat tortuous walls. There are numerous stomates distributed equally over the lower and upper surfaces. In the region of the petiole the epidermal cells become elongated, while the stomates become fewer and finally disappear. The conducting tissue is represented by fine collateral bundles which run longitudinally between spongy parenchyma and palisade tissue.

Both root and hypocotyl are terete. The center is occupied by a thin strand of primary vascular tissue, which is inclosed by a cortex and bounded at the periphery by a single-layered epidermis. The epidermis in the apical root region is specialized, in that many of its cells are elongated to form hairs. The epidermis of the hypocotyl is cuticularized and, like the older root zone, is devoid of hairs.

The cortex is made up of three to seven rows of elongated barrel-shaped cells which are separated from one another by large intercellular spaces (fig. 12). The innermost layer of the cortex contains smaller and more regular cells; some of which contain crystal sand. Cortex and vascular tissues are separated by an endodermis. The cells composing this layer are four-sided and regular, and there are no intercellular spaces among them (fig. 12, D). The root tip, with the exception of the first few millimeters, has a primary endodermis which is characterized by the Casparian strips along the radial walls. Plaut (9) made a special study of the development of the endodermis of the sugar beet, and his findings were substantiated by this investigation. The primary endodermis extends axially over a distance of 3 centimeters, when it becomes secondary, which state is characterized by the development of a suberin lamella over the entire surface. The cells of the endodermis which lie opposite the protoxylem points pass into the secondary state later than the cells in the other regions. In the lower region of the hypocotyl the endodermis becomes primary again and finally disappears. In somewhat older seedlings, according to Rüggeberg (10), the primary endodermis extends within a few millimeters of the apex of the hypocotyl and assumes the secondary state as soon as the cortex no longer offers protection to the vascular tissue.

The central cylinder of root and lower hypocotyl is made up of a diarch protoxylem plate with alternating phloem groups, a single-layered pericycle, and a band of parenchyma between xylem and phloem (fig. 13). In the upper hypocotyl, however, phloem and xylem form collateral bundles while the center of the stele is occupied by a pith (fig. 14, B; fig. 18, B). The change in the arrangement of the vascular tissue which takes place in the upper hypocotyl is described in detail later.

The pericycle of the young stele forms a single-layered concentric ring next to the endodermis (fig. 13). Its cells are uniform in shape and more or less rectangular. Its embryonic progenitors are like the other parenchyma cells. Soon, however, they begin to divide and elongate axially. They remain small in cross section while the cells of the endodermis greatly enlarge.

Differentiation of the primary vascular tissue takes place close behind the growing region. Here the procambium forms a dense

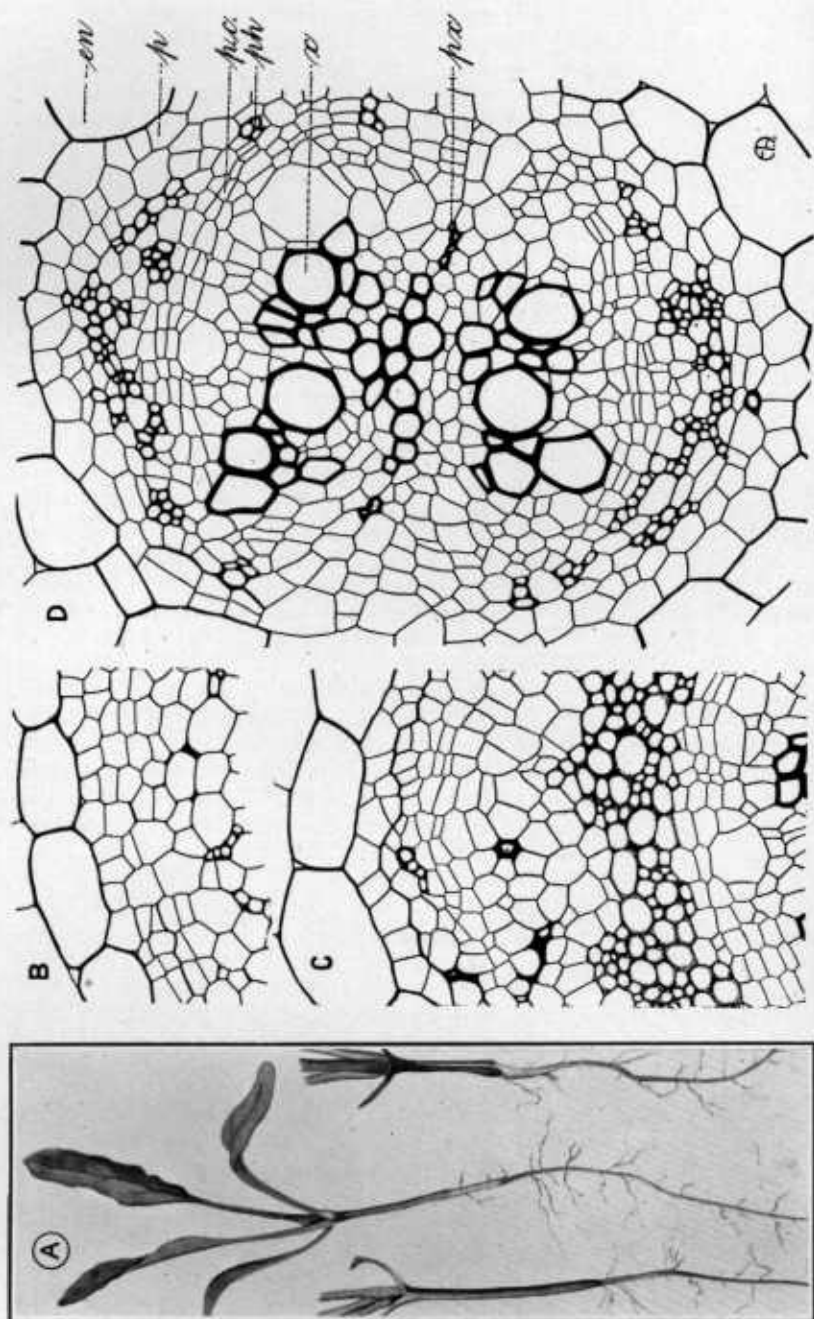


FIG. 12.—A. Best seedlings about 15 days old. Seedling at the right shows the beginning of the sloughing off of the cortex. B. Development of a supernumerary cambium from cells of the pericycle. $\times 305$. C. Development of a supernumerary cambium from the cells of the phloem parenchyma. $\times 305$. D. Cross section through vascular tissue of young seedling. No supernumerary cambium has yet been formed. en, endodermis; p, pericycle; p.c., primary cambium; p.v., phloem; x, xylem; p.z., protoxylem. $\times 305$.

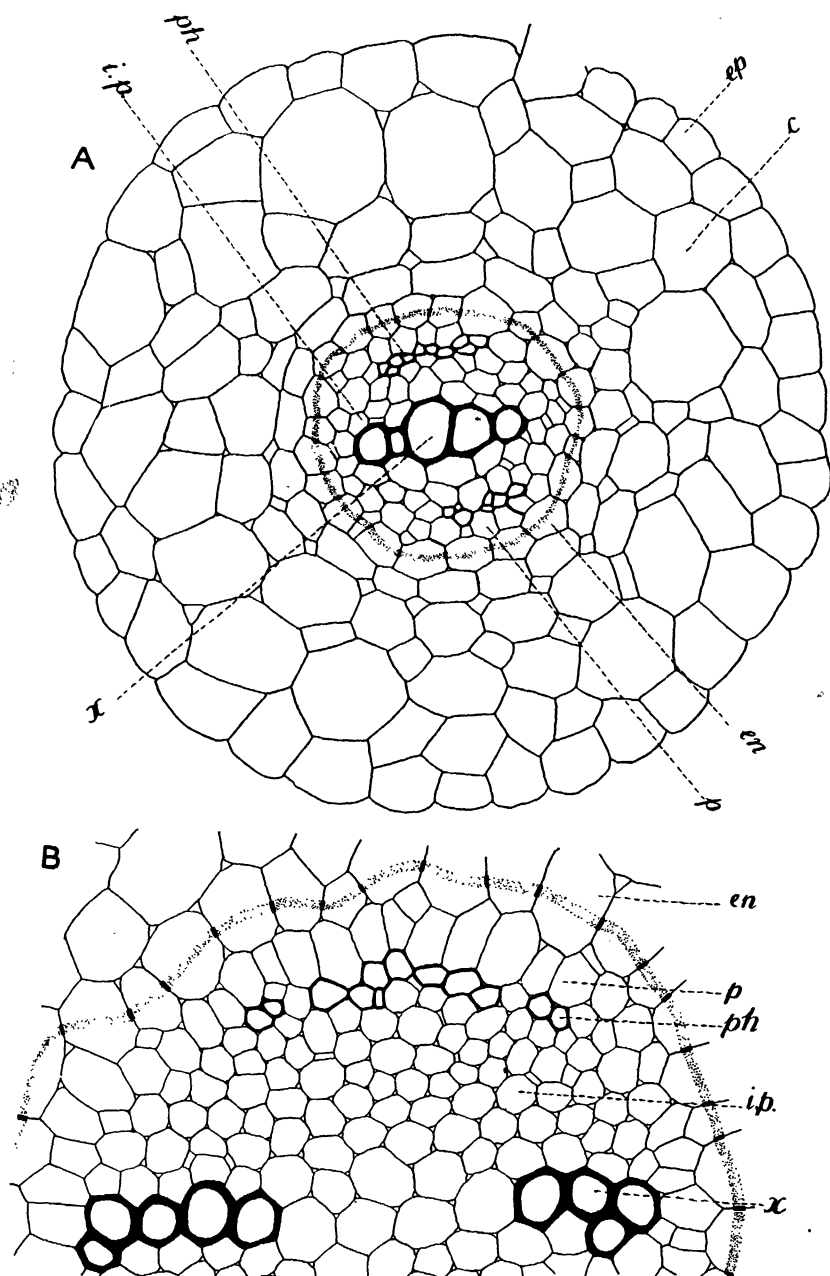


FIG. 13.—A. Cross section through young beet seedling. $\times 355$. c, cortex; ep, epidermis; en, endodermis; ph, phloem; i. p., interstitial parenchyma; p, pericycle; x, xylem. B. Partial cross section of young beet seedling. $\times 476$. The interstitial parenchyma in which the primary cambium originates is much more developed here than in A

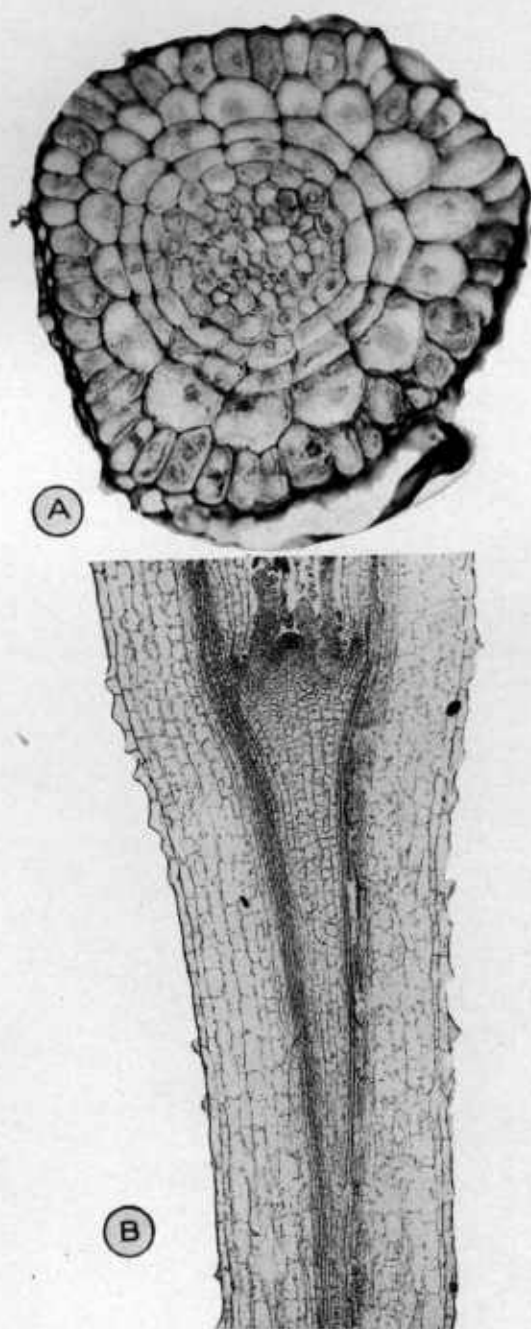


FIG. 14.—A. Cross section of young beet root. $\times 465$. Note the formation of the first two sieve tubes of the vascular tissue. (See legend of Figure 15, A, for identification of issues.) B. Median longitudinal section of young seedling. $\times 46$

tissue composed of elongated thin-walled cells. Specialization in these cells begins at a distance of about 2 millimeters from the calyptragen. Two cells, lying adjacent to the pericycle and separated from one another by an angle of 180 degrees, have enlarged and divided to form the first sieve tubes and companion cells of the primary phloem (fig. 14, A; fig. 15). The sieve tube commonly abuts on the pericycle, but in the upper hypocotyl, according to Seeliger (13), the companion cell lies adjacent to the pericycle and the sieve tube next to it. Soon after the first phloem cells have differentiated, two other procambium cells which lie to the right and left of the sieve tubes undergo changes and mature into the first elements of the protoxylem. Differentiation in the protoxylem progresses centripetally until the two protoxylem points meet in the center to form the primary xylem plates. From now on xylem cells mature to the right and left of the xylem plate until all the cells of the primary wood have been formed (fig. 16). The first-formed xylem cells are narrow elongated elements with sloping or transverse end walls. They have secondary wall thickenings in the nature of rings or spirals. The later-formed cells are larger

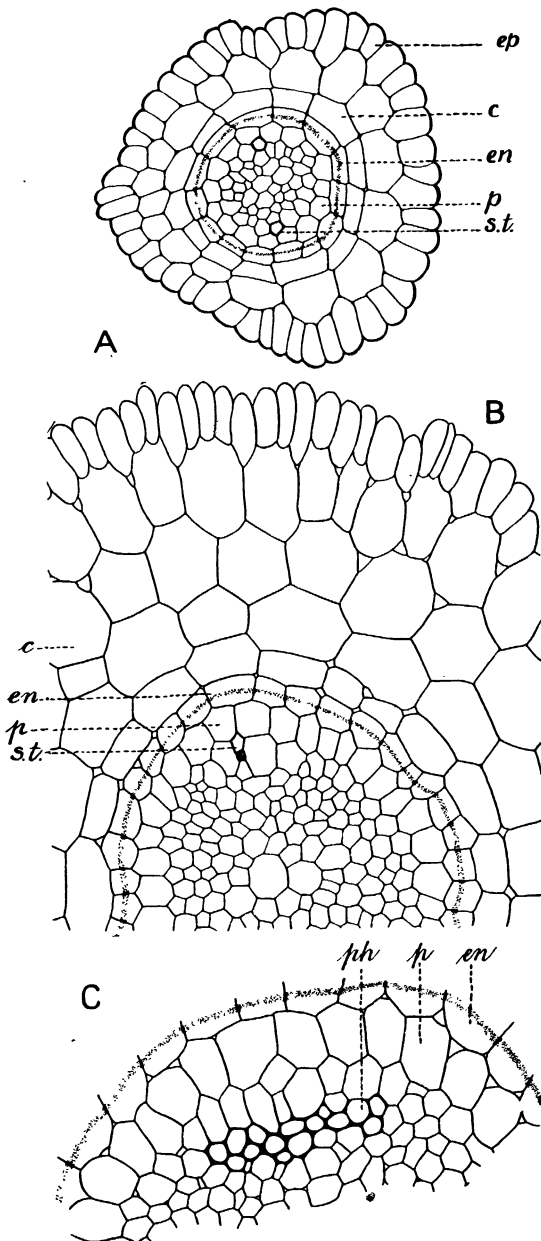


FIG. 15.—A. Cross section through young seedling root of beet. $\times 335$. *ep*, epidermis; *c*, cortex; *en*, endodermis; *p*, pericycle; *s. t.*, sieve tube. Notice that the cortex is very narrow. B. Cross section through large seedling root of the same age. $\times 335$. The first sieve tube and companion cell have differentiated, but no xylem. C. Cross section of a somewhat older root. $\times 580$. Note the increase in the amount of phloem

in cross section but shorter longitudinally. They are reticulate or form transition stages to the spiral or ringed forms. The first-formed xylem elements are the protoxylem while the later-formed cells constitute the metaxylem of the primary wood.

Differentiation in the phloem is less readily followed, because of the small size of the elements. Seeliger (13) states that the metaphloem differentiates from procambium one or more cells to the inside of the pericycle. This later-formed phloem is made up of sieve tubes, companion cells and phloem parenchyma. In the region of the hypocotyl, xylem and phloem form collateral bundles in which the protoxylem is endarch. The change from the exarch condition in the root to the endarch condition in the upper hypocotyl is very abrupt, with the transition region extending over only a few millimeters. In this process, progressively differently situated procambium cells mature into vascular tissue. The two poles of the xylem plate, which in the root meet in the center, become separated, because of the failure of the procambium in this region to

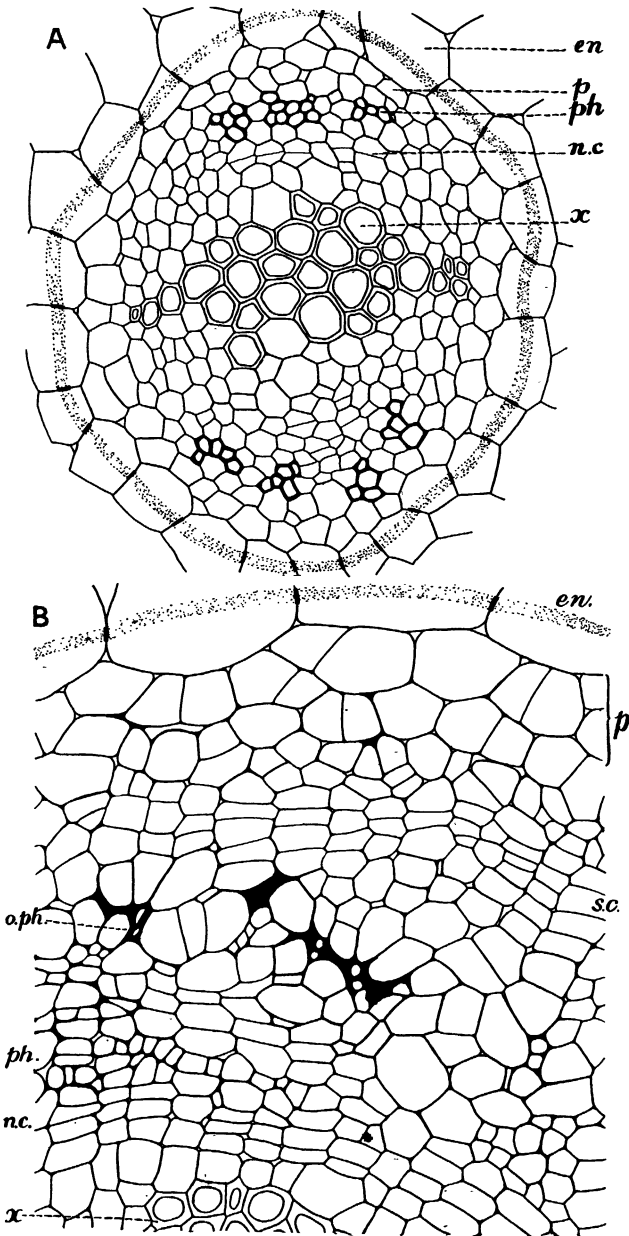


FIG. 16.—A. Cross section through young beet seedling root, showing development of primary xylem plate and the initiation of the primary cambium. *en*, endodermis; *p*, pericycle; *ph*, phloem; *n.c.*, normal primary cambium; *x*, xylem. $\times 373$. B. Cross section through older seedling, showing development of the secondary cambium. *en.*, endodermis; *p*, pericycle; *s.c.*, secondary cambium; *o.ph.*, obliterated protophloem; *ph.*, phloem; *n.c.*, normal primary cambium; *x*, xylem. $\times 373$

mature into xylem elements. Xylem differentiation becomes instead more prominent on either side of the two strands whereby the latter change their shape at first to triangular (fig. 17) and then to oval. Later-formed elements appear more and more to the inside until in the upper region of the hypocotyl the change from the exarch to the endarch arrangement has been completed. The phloem is also affected in this change from root to stem structure. The two phloem groups become divided, each forming two strands. Then two and two halves of opposite groups approach each other and come to lie external to the xylem with which they now form collateral bundles. While the central cylinder increases in size the cells of the cortex

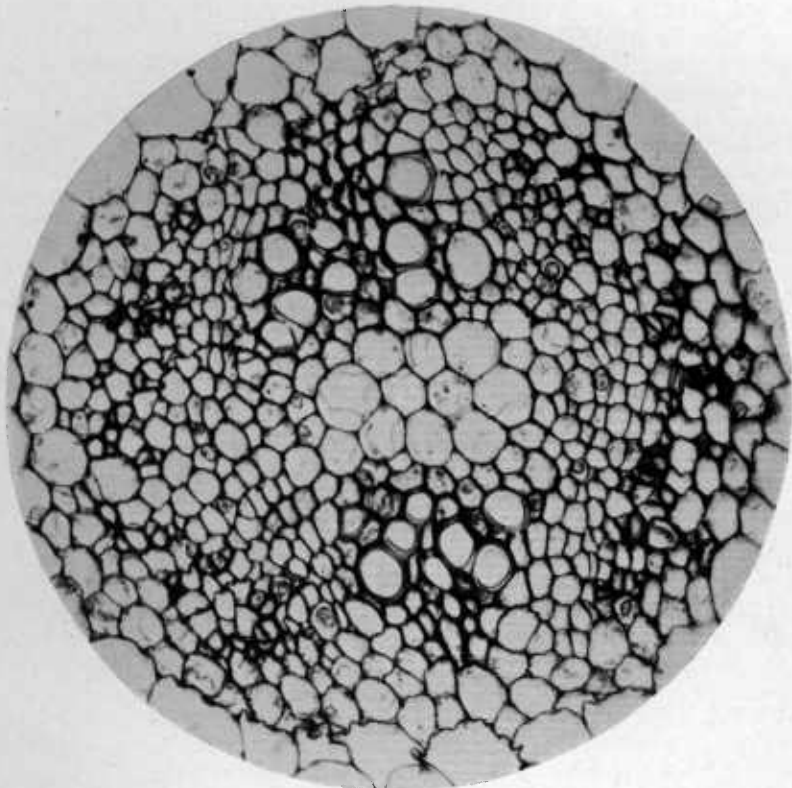


Fig. 17.—Cross section through hypocotyl of beet seedling. The xylem is changing from the exarch to the endarch condition. $\times 435$

grow but little. They are at first passively stretched but later rupture and collapse. These changes are externally visible by the appearance of fine fissures which gradually widen, and finally the cortex is sloughed off.

This process takes place earlier in the root region than in the hypocotyl. In the latter the changes in the cortex due to radial expansion of the stele cause first an extension of the endodermis from the lower hypocotyl to the immediate vicinity of the growing region of the crown. Concomitant with the sloughing off of the cortex is the development of a periderm, which takes over the protective function of the primary cortex. Since the protoxylem is

formed in a region where there is much change and enlargement in radial and tangential directions, the elongation of the surrounding tissue causes the rings of the elements to be pulled farther apart, and, as the stretching continues, the cells may be flattened until the lumen is closed. Metaxylem and wood-parenchyma remain unchanged, but, according to Seeliger (13), suffer displacement due to radial contraction of the root, which takes place simultaneously with the development of the secondary tissues.

SECONDARY GROWTH

The primary growth of the beet is concluded with the appearance of the second pair of leaflets; this normally takes from 10 to 12 days after the seed is planted. The largest diameter of the beet at that stage is at most only a few millimeters, while that of the mature beet is 15 centimeters or more. This increase in thickness is the result of cambial growth accompanied by independent cell division and cell enlargement of the parenchyma.

Cambial activity embraces two distinct phases: Differentiation and growth of the primary cambium and development of secondary cambiums. The primary cambium forms the innermost annular zone in the beet, while the secondary cambiums form a large number of supernumerary rings, of which, however, only the inner five or six mature their tissues. Since the origin of the primary and secondary cambiums differ, their development will be studied separately.

DEVELOPMENT OF THE PRIMARY CAMBIUM

In the following description, unless stated differently, the anatomical picture is that of the lower hypocotyl or upper root region. Since growth and maturation of the tissues takes place acropetally, sections lower down will give younger developmental stages, those higher up more advanced ones.

When a seedling is about 10 days old and the second pair of leaflets becomes visible (fig. 12, A), the parenchyma cells between the primary xylem and phloem begin to elongate axially and undergo tangential division. A new meristematic zone thus arises which becomes the primary cambium and as such develops xylem and phloem in the normal manner. This cambium appears at first in the region of the two phloem poles, but gradually extends laterally over the two protoxylem points. In the latter case, however, the divisions which give rise to the cambium take place in the pericycle.

The xylem formed by the cambium unites intimately with the metaxylem of the primary wood (fig. 18, A). Occasionally, according to de Bary (1), a layer of parenchyma is interpolated between primary and secondary xylem. The zone in front of the protoxylem points remains free from secondary xylem; here the cambium forms parenchyma tissue which forms the two primary medullary rays.

Simultaneously with the formation of secondary xylem, the cambium is forming phloem centrifugally. This secondary phloem, like the xylem, becomes continuous with the primary tissue and indistinguishable from it (fig. 12, D). While the secondary phloem is forming, the primary phloem parenchyma enlarges and divides, thereby forcing the groups of sieve tubes apart; and since the latter have ceased development, they are at first stretched and finally obliterated

(fig. 12, C). The primary cambium continues active growth, but its office is soon to be yielded to another meristematic layer—the secondary or supernumerary cambium.

DEVELOPMENT OF THE SECONDARY CAMBIUM

The origin of the secondary cambium is not uniform for different regions of the beet, and even similar regions show pronounced deviations. The situation is perhaps best portrayed by the following remark of Secliger (13) in the summary of his detailed ontogenetic studies: "In the development of supernumerary tissues it is not the morphological origin of a cell but its topographic relation to the axis and the neighboring tissues which determines its future."

In the early development of the seedling the first phloem cells develop adjacent to the pericycle, and the later developed metaphloem is separated from the pericycle by a single layer of undifferentiated procambial tissue. The cells of this layer enlarge and subsequently divide, thereby interpolating an ever-widening band of parenchyma between pericycle and phloem (fig. 15, B). This band of

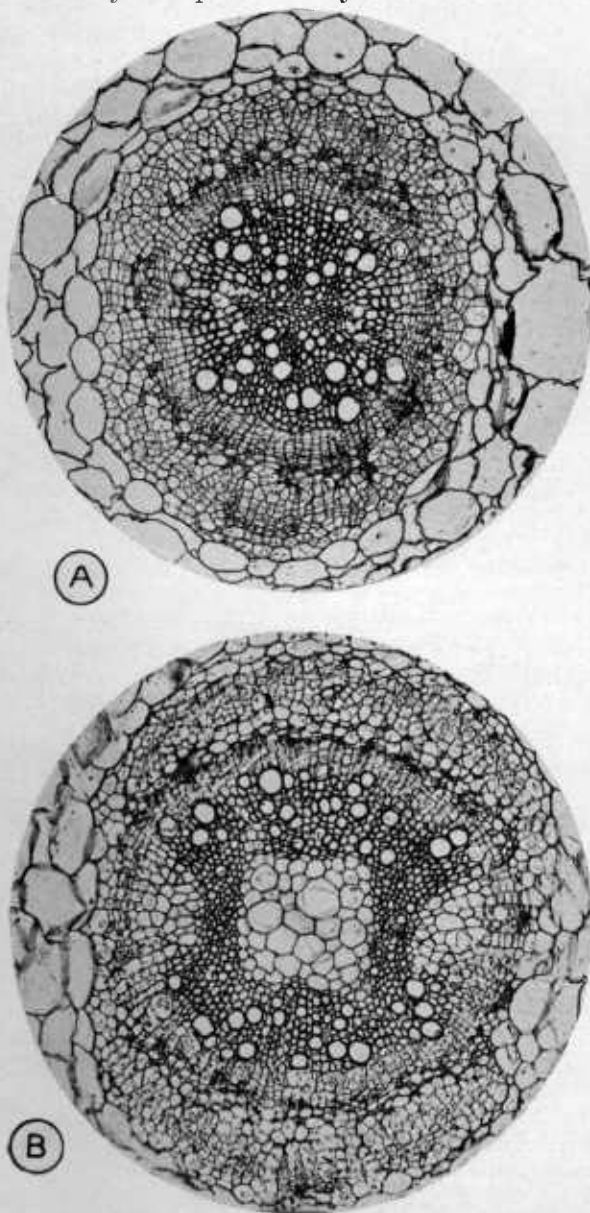


FIG. 18.—A. Cross section through a young beet seedling, showing development and activity of the primary and secondary cambiums. $\times 85$. (See legend of Figure 16, B, for identification of tissues.) B. Cross section through the upper hypocotyl of the same seedling. $\times 85$

parenchyma is not of uniform width, partly because cell division in the primary phloem parenchyma causes certain of the phloem groups to remain close to the pericycle. Seeliger does not mention this mode of development, but derives all this tissue from divisions in the phloem parenchyma. Soon there appear periclinal division walls in certain cells of this band, initiating the development of a secondary cambium. In the region of the protoxylem points, of course, the secondary cambium originates just as does the primary one in the pericycle (fig. 12, B).

This mode of development is characteristic for the root and the lower hypocotyl. In the upper hypocotyl the cambium arises altogether in the pericycle, while the central hypocotyl shows transition stages with more and more pericycle cells taking part in cambium formation as the apical region is approached.

Once initiated the cambium will produce an annular zone of bundles and parenchyma tissue. Since, however, additional cambiums are formed, the behavior of the first cambium initial differs from the normal behavior of cambium cells. When the cambium initial undergoes the first division, the outer of the two daughter cells becomes the initial of a new supernumerary cambium; while the inner daughter cell divides further and produces xylem, phloem, and medullary ray tissue. This process is repeated until all supernumerary cambiums have been formed. However there is no uniform method governing the formation of the supernumerary cambiums. Often sections of two supernumerary cambiums originate simultaneously, one from an inner, the other from a more peripheral phloem parenchyma cell. Since most of the supernumerary cambiums of the beet are initiated in quick succession, a beet no thicker than a pencil contains practically all annular zones of growth developing simultaneously.

PERIDERM DEVELOPMENT

The periderm of the beet always develops from cells of the pericycle. Its formation is initiated when the seedling has about five pairs of leaves, that is, at a time when the supernumerary cambiums are forming and the primary cortex is being sloughed off, and since this process takes place first in the root zone, the periderm develops acropetally, extending gradually into the hypocotyl. Periderm development begins with a conversion of the cells of the pericycle, by tangential divisions, into a band of meristematic tissue, which constitutes the phellogen or cork cambium. From the phellogen are formed, by reciprocal division, cork cells outside and phelloderm cells inside. The number of phelloderm cells, however, is smaller than the number of cork cells, since the latter are constantly being sloughed off and must be replaced. On the whole the periderm forms a thin covering from five to eight cells wide (fig. 19). The individual cork cells have the form of a parallelepiped with a five or six sided base. The height is less than the diameter of the bases, thus giving the cells a flattened appearance. The walls of the periderm cells are thin and suberized, except the middle lamella which is lignified.

DEVELOPMENT AND GROWTH OF THE ANNUAL RINGS

As previously stated, the peculiar zonation noticed in a cross section of a beet is produced by concentric rings of vascular tissue inclosing broad bands of parenchyma. Near the periphery, however,

the rings are very narrow and the tissues just in the process of differentiation (fig. 20). By examining the different rings in centripetal order, one can easily follow out the ontogeny of a ring.

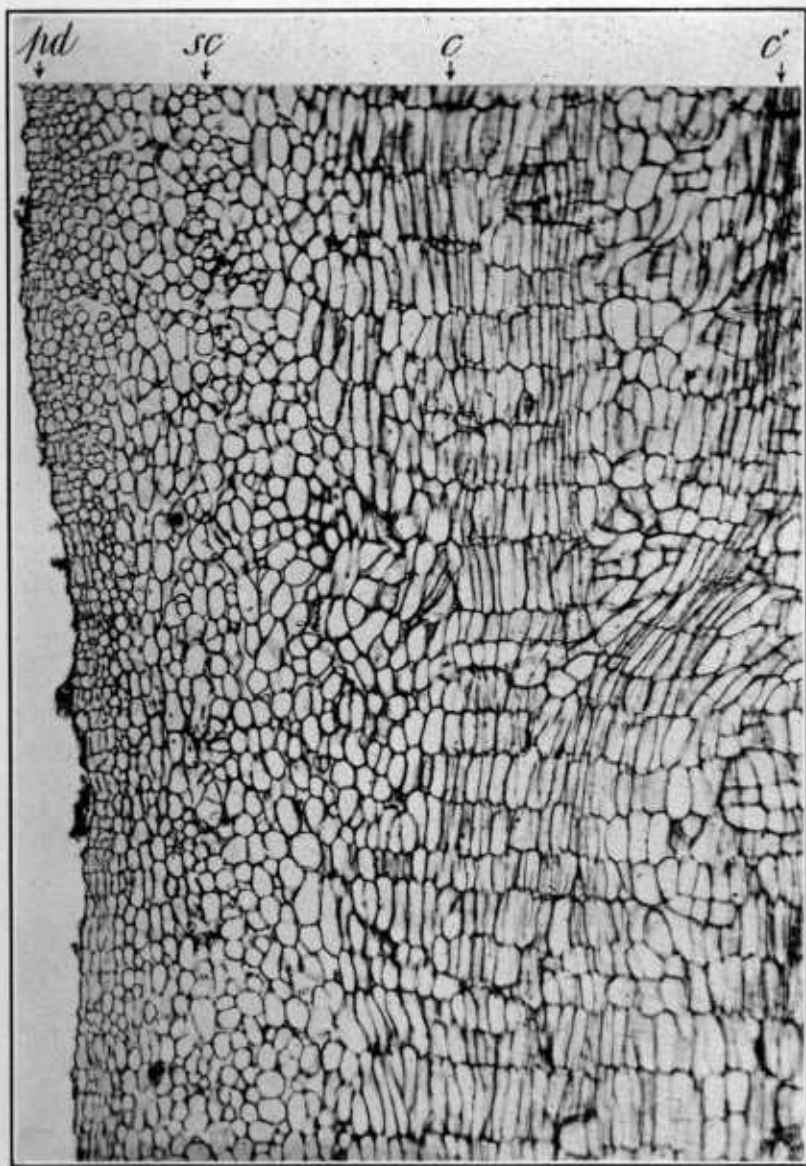


FIG. 19.—Radial section through periphery of mature beet, showing periderm, cortex, and cambium of the first ring. *pd*, periderm; *sc*, secondary cortex; *c*, cambium; *c'*, cambium of second ring.
× 270

The development and growth of the individual rings follows, in principle, the differentiation processes of ordinary collateral bundles, but these are modified because of the interpolation of large amounts of storage parenchyma inside the bundles.

The youngest ring, nearest the periphery, is composed of a multi-seriate cambium in which here and there a few cells have matured into small groups of sieve tubes and companion cells (fig. 21). In the second ring phloem differentiation becomes quite general, and

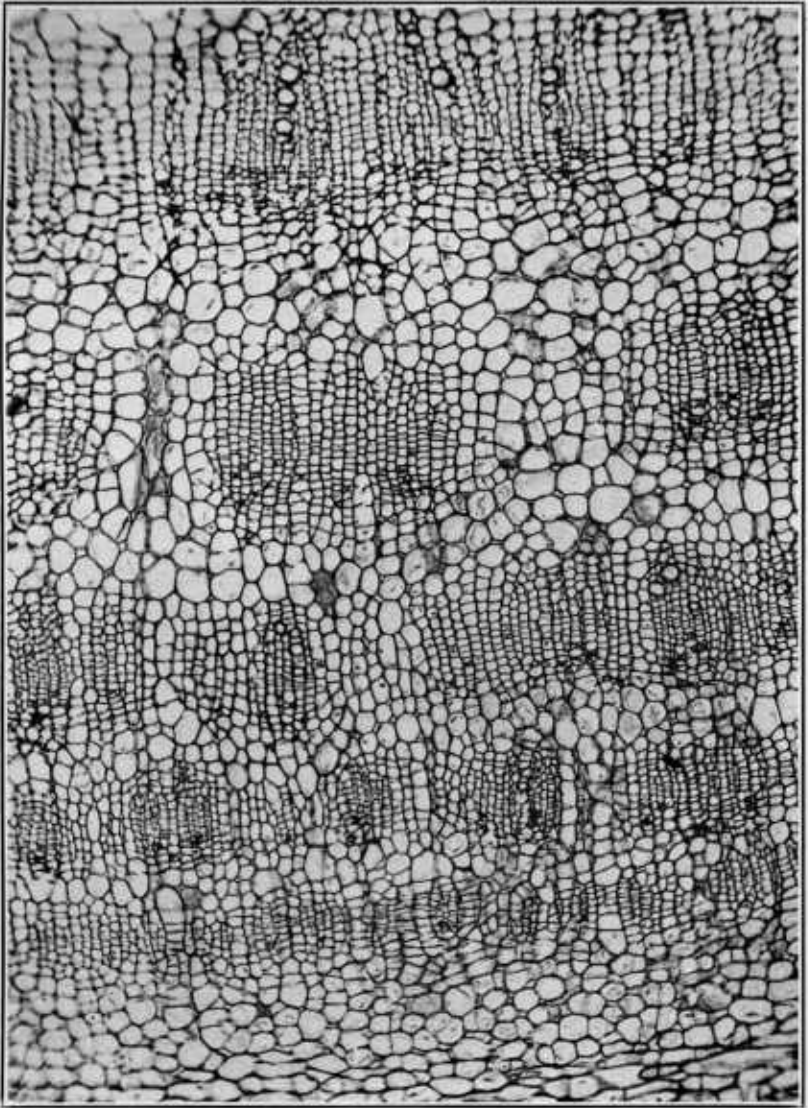


FIG. 20.—Cross section of peripheral zone of mature heet. The rings are composed mostly of undifferentiated cambium and some phloem. $\times 90$

even in subsequent ones the extensive development of phloem dominates the anatomical picture. Following the differentiation of the first sieve tubes, phloem parenchyma is formed, and this subsequently divides and enlarges, pushing the first-formed groups of sieve tubes farther away from the vascular ring and finally obliterating them.

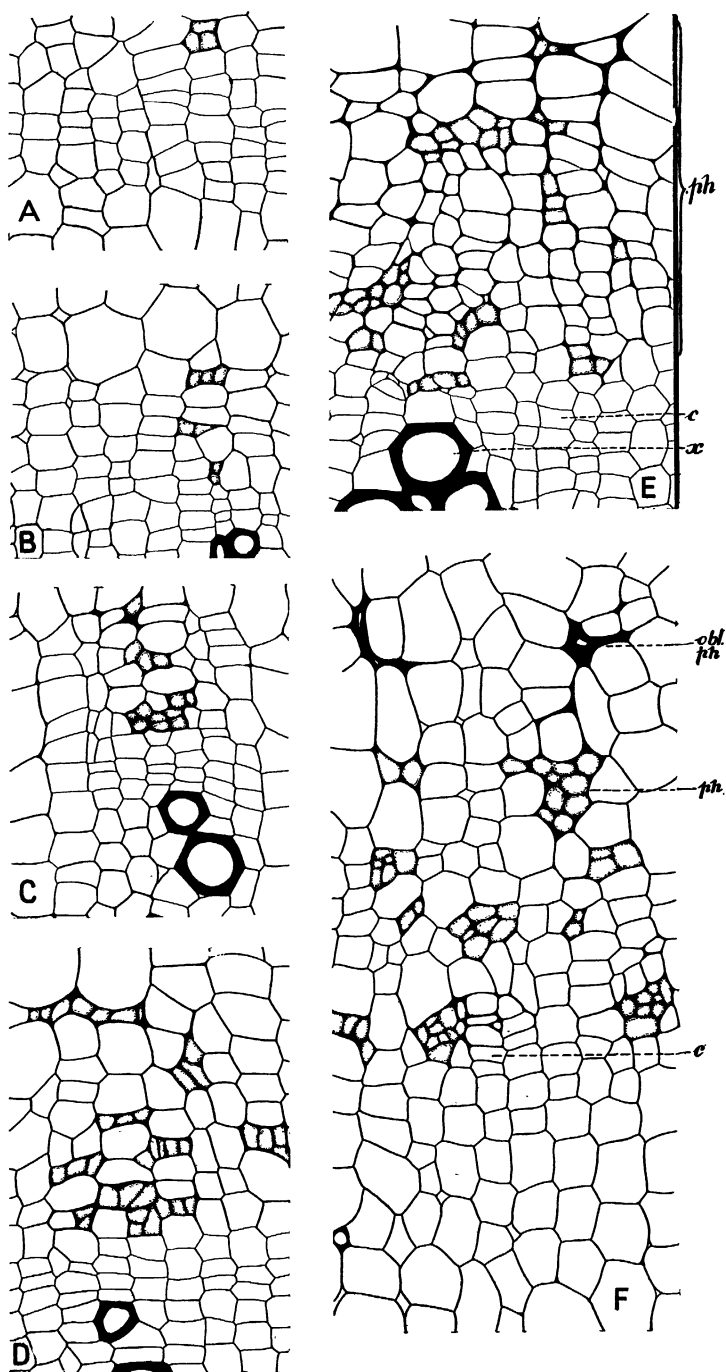


FIG. 21.—Ontogeny of the phloem of sugar beet. $\times 317$. A, first peripheral ring; B, second ring; C, third ring; D, fourth ring; E, fifth ring; F, fifth ring, but from a different part of the beet. The phloem shows a very marked degree of development compared to the xylem. The outermost phloem groups in F are already obliterated. $\times 320$

In general, the groups of sieve tubes appear in narrow radial bands broken up radially and tangentially by the larger cells of the phloem parenchyma.

Centripetally the cambium develops a broad band of parenchyma in which appear the first xylem cells; this occurs usually only after considerable phloem has been formed. In certain bundles, phloem and xylem differentiation appears to be reciprocal, but most often the appearance of xylem is belated. After the first few xylem cells have been formed, the cambium matures additional parenchyma and occasionally a xylem cell. Cell division in the parenchyma between the xylem continues irregularly, and as a result the xylem cells became displaced radially and tangentially and project far into the parenchyma (fig. 22). The cambium between the bundles gives rise to large-celled medullary-ray tissue. Where bundles are very close together the ray cells are small and radially elongated.

The rings of vascular tissue are separated by broad bands of storage parenchyma. In the peripheral zone these bands are not more than one or two cells wide, and in places the phloem of the next inner ring abuts on the cambium of the outer ring (fig. 23). Since each supernumerary cambium is the direct descendant of the next older cambium, and since the first-differentiated phloem groups are sieve tubes, the band of interzonal parenchyma is ultimately the product of centripetal cambial growth.

A close examination of the interzonal parenchyma shows that it is in reality made up of three regions: An outer, comparatively broad zone, containing scattered xylem cells; an intermediate, purely parenchymatous zone; and an inner zone containing obliterated phloem (fig. 2, A). As xylem differentiation is strictly centripetal the innermost xylem cells constitute the inner limit of the first zone, which is thus closely related to the vascular ring. The broad intermediate zone has been formed by cell division and cell enlargement of the parenchyma cells differentiated by the cambium previous to xylem formation. Finally, the inner zone is delimited centrifugally by the obliterated phloem and consists chiefly of phloem parenchyma. It is therefore the product of centrifugal growth of the older ring.

SUMMARY

The sugar beet is an elongated more or less pear-shaped body composed morphologically of crown, neck, and root. In cross section it appears to be made up of a number of annular zones or rings of growth, separated by bands of storage parenchyma. Only the four or five inner rings mature their tissues, while the peripheral ones remain in a more or less meristematic condition.

The center of the beet is occupied by a solid, more or less star-shaped, core of which the innermost part constitutes the primary xylem plate. The latter is either directly continuous with the secondary xylem of the core, or is separated from it by a concentric ring of parenchyma of varying width.

The young seedling beet has a central strand of vascular tissue inclosed by a cortex and bounded at the periphery by an epidermis. The central strand is made up of a diarch protoxylem plate with alternating phloem groups, a single-layered pericycle and a band of interstitial parenchyma between xylem and phloem.

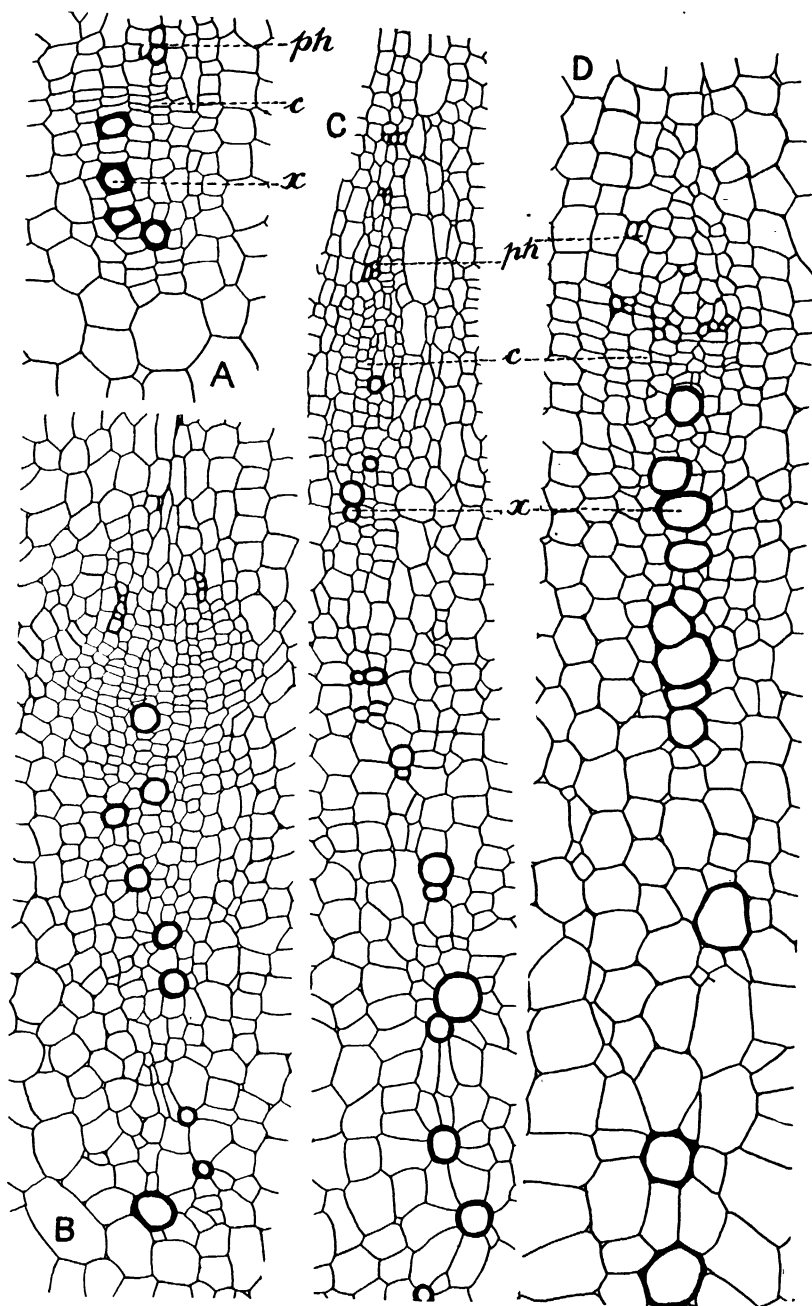


FIG. 22.—A. Young peripheral bundle of mature beet. $\times 510$. *ph*, phloem; *c*, cambium; *x*, xylem. B. Older bundle, with parenchyma developing between the xylem cells. $\times 100$. C. Very narrow bundle of the same age. A large amount of parenchyma has become interpolated between the vessels, forcing them farther and farther apart. $\times 100$. D. Bundle of an older ring, which shows a larger amount of xylem. $\times 180$

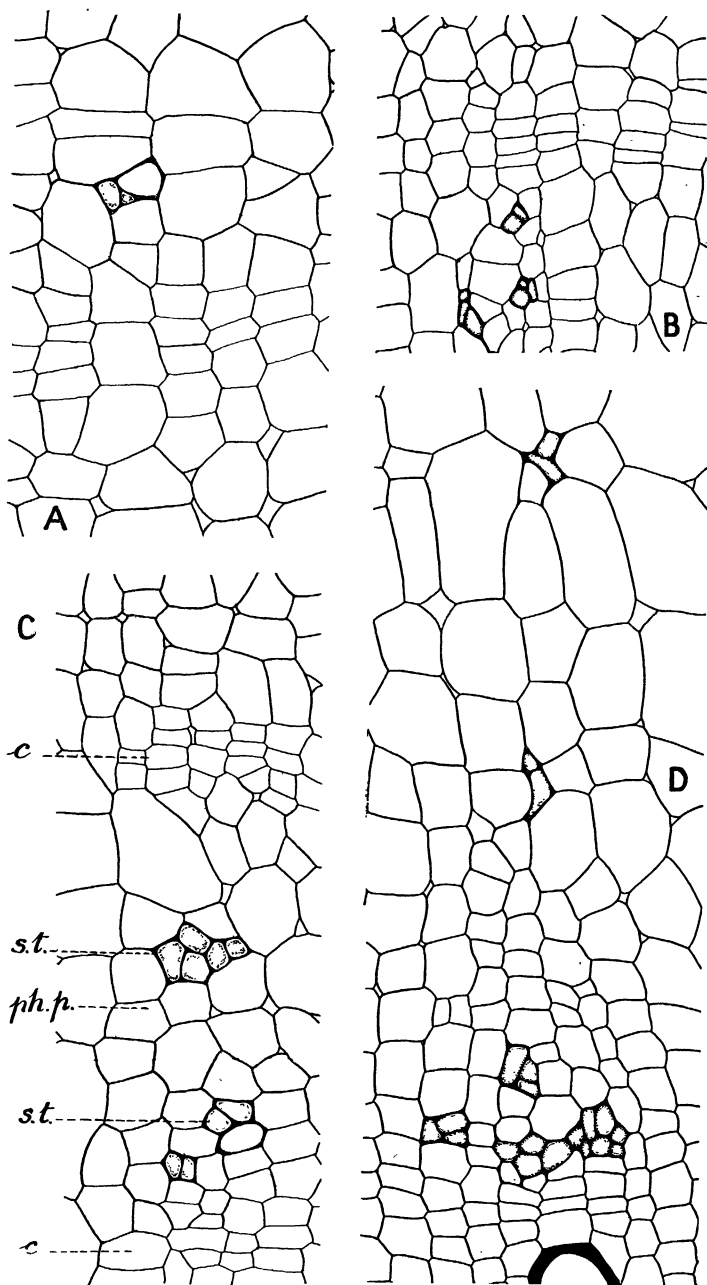


FIG. 23.—Ontogeny of the interzonal parenchyma of beet. A. Peripheral zone of an actively growing beet. The outermost ring comprises only one layer of cambium. The cambium of the second ring has already formed a group of sieve tubes and parenchyma. Note that the group of sieve tubes lies next to the cambium of the first ring. B. A more advanced stage than in A. C. The outer cambium has formed parenchyma centripetally. In the next inner ring the first sieve tubes have become separated from later-formed ones by phloem parenchyma cells. *c*, cambium; *s. t.*, sieve tube; *ph. p.*, phloem parenchyma. D. A more advanced stage. The first-formed sieve tubes project far into the parenchyma of the ring.

Secondary growth of the beet involves the activity of a primary cambium and of secondary cambiums.

The primary cambium gives rise to the innermost annual ring in the beet. It arises in the interstitial parenchyma, except, of course, in the region opposite the two protoxylem points where it is derived from the pericycle.

The first secondary cambium arises in root and lower hypocotyl from cells of the primary phloem parenchyma. Occasionally undifferentiated procambium cells between pericycle and phloem parenchyma contribute to its development. In the upper hypocotyl it is derived from the pericycle, and in the intermediate hypocotyl both pericycle and phloem parenchyma contribute to its development. In the region opposite the protoxylem points, both primary and secondary cambiums are descendants from pericycle tissue.

All other supernumerary cambiums stand for the most part in direct lineage with the first secondary cambium.

The periderm is derived from the pericycle. It forms phellogen and phelloderm cells in reciprocal fashion.

Practically all the supernumerary cambiums for the annular rings of the mature beet have been formed while the latter is no thicker than a lead pencil. The enormous increase in the diameter of the beet is due to cell division and cell enlargement taking place simultaneously in all the rings.

The degree of development attained by the vascular tissue of a ring and the separating band of interzonal parenchyma varies greatly with different beets. In any given one, however, the innermost rings have the broadest band of parenchyma.

The interzonal parenchyma in its entirety is made up of three regions: An outer zone containing scattered xylem cells, a central purely parenchyma zone, and an inner zone containing obliterated phloem. The first two zones have been formed by centripetal growth of the outer ring, while the third zone is the product of centrifugal growth of the older inner ring.

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